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POLLEN APERTURE VARIATION AND PHYLOGENY IN  
*DICENTRA* (FUMARIACEAE)

KINGSLEY R. STERN

*Dicentra* Bernh., comprising some 20 species of perennial and biennial herbs and climbers of North American and East Asian distribution, was monographed by Hutchinson (1921) as part of a larger treatment. Fedde (1936) largely followed Hutchinson's treatment in his discussion of the Papaveraceae, although both earlier works were incomplete. In my revision of the genus (1961; 1967), phylogenetic trends, based primarily on morphological and anatomical features, were discussed. Berg (1964), studying seed dispersal ecology in *Dicentra* independently, reached essentially similar conclusions about the intrageneric phylogeny, as did Fahselt and Ownbey (1968) while investigating the flavonoid components. Cytological evidence obtained by Ryberg (1960), Ernst (1965), Stern (1968) and others suggests the development of a polyploid series accompanying morphological and chemical advancement, but further extensive study is needed before the role of polyploidy in the evolution of the genus, and cytotaxonomic interrelationships in general can be clearly portrayed.

After brief mention of pollen morphology in my 1961 monograph, I studied *Dicentra* pollen grains in more detail (Stern, 1962), and found the interspecific variation not only extensive, but specifically constant enough to permit distinguishing between all except two of the species on the basis of pollen morphology alone. Such interspecific variation is exceptional, although not wholly unique, as the representative studies of Dahl (1952), Fasneder (1959), Helmich (1963) and Lewis (1965) suggest. My 1962 study included descriptions and dimensions of the pollen grains and mention of phylogenetic trends. This study amplifies

and details the extensive aperture variation found, indicates correlations between pollen morphology and other features, and, on the basis of new evidence, revises some phylogenetic concepts.

Pollen grains for this study were mounted in lactic acid (ca. 85%), after removal from herbarium specimens, and slides were made semi-permanent by the addition of ringing cement and cover glasses. Additional mounts in Dahl's medium (Stern, 1961), Calberla's solution, silicone oil (Anderson, 1960) and glycerine jelly, following acetolysis, (Erdtman, 1960) were made for comparison, although it was found that the latter preparations were of more value in exine studies than in aperture studies. A duplicate set of acetolyzed pollen slides has been deposited in the collections of the Palynologiska Laboratoriet, Stockholm-Solna, Sweden.

*D. burmanica* Stern: *Kaulback 267* (BM, E).

*D. canadensis* (Goldie) Walp.: *Hone 179* (MIN); *Shafer 130* (UC); *Stern 190* (UC); *Stern 192* (UC); *Umbach 1570* (S).

*D. chrysantha* (H. & A.) Walp.: *Bacigalupi & Holmgren 3179* (UC); *Meyer 745* (UC); *Sharsmith 4277* (S); *Sowder 431* (UC); *Stern 157* (MIN); *Van Dyke s.n.* (CAS, F, POM).

*D. cucullaria* (L.) Bernh.: *Anderson 661* (UC); *Bush 13228* (S); *Nielsen 2399* (MIN); *Stern 191* (UC); *Stern 193* (UC); *Umbach s.n.* (F, MICH, UC, US, WIS).

*D. eximia* (Ker) Torr.: *McVaugh 5714* (UC); *Stern 2021* (UC); *Stern 197* (UC); *Stern 202* (UC).

*D. formosa* (Haw.) Walp.: *Brown s.n.* (MIN); *Everett & Balls 9458* (S); *Henry s.n.* (DS); *Kruckeberg 4990* (UC); *Leach & Leach 1360* (ORE); *Stern 775* (UC).

*D. grandifoliolata* (Merrill) Stern: *Ward 143* (*Vernay-Cutting Expdn.*) (GH, NY).

*D. lichiagensis* Fedde: *Handel-Mazzetti 4329* (GH, US); *Maire 3265B* (UC); *Schneider 2004* (B, US); *Tsai 56060* (AAH).

*D. macrantha* Oliv.: *Forrest 26601* (E, NY, W, US); *Smith 2098* (UPS).

*D. macrocapnos* Prain: *E.I.C. Kew Distr. No. 119* (GH, K, L, LE, M, S); *Stainton, Sykes & Williams 4254* (BM); *Stainton, Sykes & Williams 5009* (BM).

*D. nevadensis* Eastw.: *Cronquist 2148* (MO); *Darland s.n.* (UC); *Stern 166* (MIN).

*D. ochroleuca* Engelm.: *Clokey & Templeton 4615* (UC); *French 332* (UC); *Gifford 195* (UC); *Howell 4079* (CAS); *Pollard s.n.* (S); *Stern 158* (MIN).

*D. pauciflora* Wats.: *Brown 418* (UC); *Haddock 14* (DS, UC); *Purpus 3140* (UC); *Rowntree s.n.* (CAS).

*D. paucinervia* Stern: *Ludlow & Sheriff 15838* (BM).

*D. peregrina* (Rudolph) Makino: *Hiroe* 7054 (UC); *Jochelson* 228 (NY, S).

*D. roylei* Hook. f. & Th.: *Lace* 1516 (E); *Ten* 1367 (B).

*D. scandens* (D. Don) Walp.: *Ownbey, s.n.* (WS); *Schneider* 3244 (B); *Tsai* 52955 (GH).

*D. spectabilis* (L.) Lem.: *Bazilevski s.n.* (LE); *Maire* 2714 (UC); *Umbach s.n.* (WIS, UC, F).

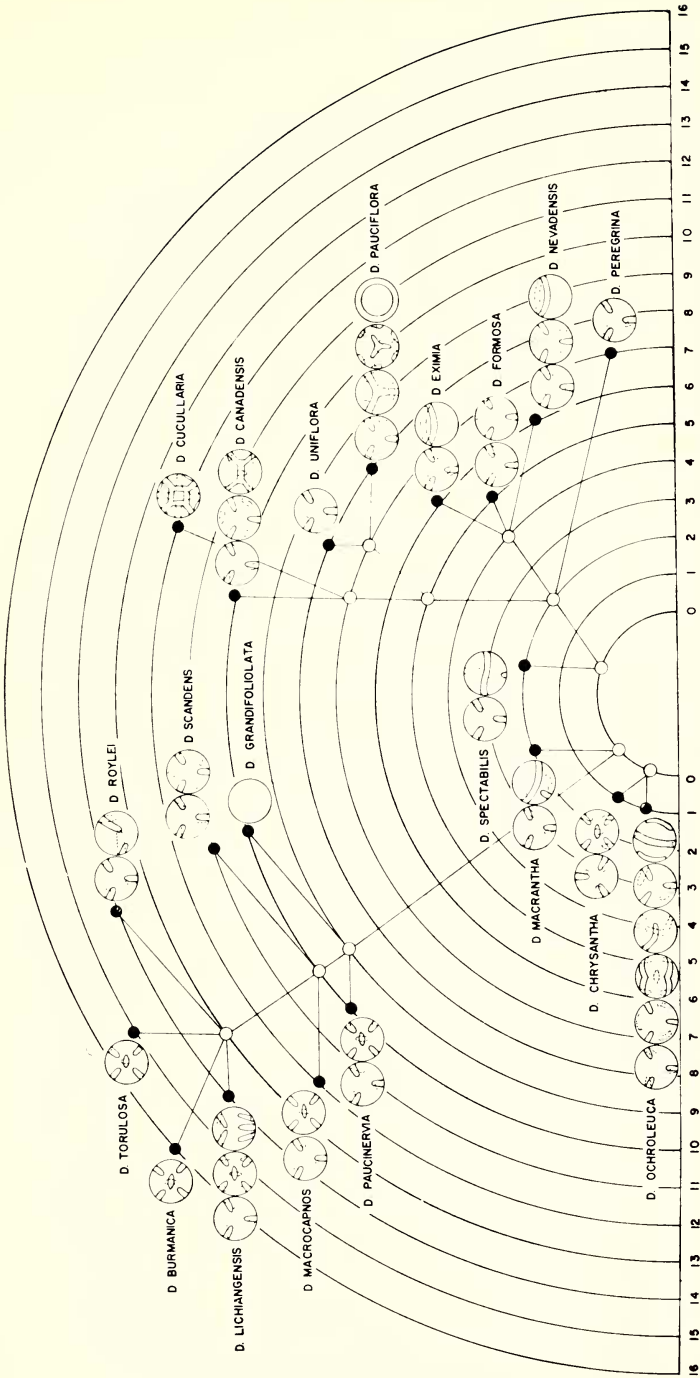
*D. torulosa* Hook f. & Th.: *Cooper* 3129 (E); *Ducloux* 948 (E); *Maire* 725 (BM, E); *Tsiang* 8866 (UC).

*D. uniflora* Kell.: *G. N. Jones* 9935 (GH); *M. E. Jones s.n.* (POM, UC); *Steward & Gilkey* (OSC).

Figure 1 illustrates, via diagrams, the various aperture arrangements occurring in pollen grains of *Dicentra* species. The pollen diagrams themselves are superimposed on a diagram revised and adapted from Stern (1961), which indicates presumed relationships between species, based on advancement indices derived primarily from morphology and anatomy. As observed by Alston and Turner (1963), such base diagrams do not indicate the factor of time for the assumed branching, since the angles of divergence, etc., are strictly diagrammatic, and are not intended to signify constant rates of evolution. Nevertheless, in the absence of extensive genetic and experimental evidence, they do serve a useful purpose as a framework for future investigation. As indicated earlier, since the base diagram appeared in its original form, support for many of the phylogenetic positions indicated has been derived from seed dispersal ecology studies and chemotaxonomy. An exception to this is the position of *D. spectabilis*, which was originally included in the subgenus *Chrysocapnos* Engelm. A reconsideration of the pollen exine morphology suggests its affinities lie closer to members of the subgenus *Dicentra*, and the chemical evidence presented by Fahselt and Ownbey (1968) tends to substantiate this. The morphology and anatomy of the species, however, is sufficiently distinctive to warrant its relegation to a monotypic subgeneric ranking of its own. *Dicentra macrantha* also is here accorded subgeneric ranking, since its floral morphology differs so markedly from that of other members of the subgenus *Chrysocapnos*; further, although it is not scandent, it does appear, vegetatively, to be more closely related to members of the subgenus *Dactylicapnos* (Wall.) Stern.

Subgenus **Hedycapnos** (Planch.) Stern, stat. nov. *Capnorchis* subg. *Hedycapnos* Planch. Fl. Serres 8:193. 1853. *Eucapnos* Sieb. & Zucc. Abh. Math.-Phys. Cl. Konigl. Bayer. Akad. Wiss. 3:721. 1840, non Bernh. Linnaea 8:468. 1833. *Dicentra* subg. *Chrysocapnos* sect. *Hedycapnos* (Planch.) Stern, Brittonia 13:21. 1961. Type species: *Dicentra spectabilis* (L.) Lem. Fl. Serres I. 3:pl. 258. 1847.

FIG. 1. Diagram indicating presumed phylogenetic relationships and correlations of pollen aperture types in *Dicentra*.



Subgenus **Macranthos** (Stern) Stern, stat. nov. *Dicentra* subg. *Chryso-carpnos* sect. *Macranthos* Stern, Brittonia 13:24. 1961. Type species: *Dicentra macrantha* Oliv. For further discussion and species synonymy see Stern (1961).

When the pollen aperture diagrams are added to the presumed phylogeny base diagram, (fig. 1), certain correlations between gross morphology and pollen morphology become apparent. The more primitive species possess numerically constant (3 or 6) apertures, which are also distinct. *Dicentra ochroleuca*, and occasionally *D. macrantha*, do, in addition to the basic 3 or 6 apertures, exhibit anomotreme pollen grains, often with bizarre aperture configurations, which are, however, always distinct. The proportion of aperture to non-aperture surface area in these and other *Dicentra* pollen grains appears to be more or less constant, regardless of the particular configurations or numbers of apertures. To demonstrate this mathematically in prolate spheroids with so many grain-to-grain variables would, however, be a most challenging task.

The more advanced species, in the subgenera *Dicentra* and *Dactylicarpnos*, in general, have numerically inconstant apertures, and, in the latter subgenus in particular, the apertures become less distinct. Also, in the subgenus *Dicentra*, there is a trend toward more numerous apertures, and eventual fusion of the apertures. Although an occasional anomotreme pollen grain will appear in the four most primitive species (*D. formosa*, *D. nevadensis*, *D. eximia* and *D. peregrina*), fusion of apertures has not been observed. In *D. pauciflora*, however, some pollen grains are 8-aperturate, the apertures consisting of 6 separate rugae or colpi, plus 6 more rugae coalesced into 2 triradiate apertures. In *D. canadensis*, some basically 12-aperturate pollen grains become synaperturate, and in *D. cucullaria*, various configurations, but all synperture, are typical. If increase in numbers of apertures, and fusion of apertures, as well as decreases in the distinctness of aperture margins in the pollen grains of *Dicentra* may be considered advancement, such advancement appears to have accompanied morphological and anatomical advancement in the genus.

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Department of Biological Sciences, Chico State College, Chico, California

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## FOSSIL LEAVES OF LYONOTHAMNUS

SATISH C. BANWAR

Leaves of the extant genera *Lyonothamnus*, belonging to the family Rosaceae, and *Comptonia*, belonging to the family Myricaceae, are very similar in external appearance. Many paleobotanists who have examined fossil leaves of *Lyonothamnus* were at times led to identify them as *Comptonia*. This study was conducted to examine and compare leaves of *Lyonothamnus*, both extinct and extant, and those of *Comptonia*, so that differences and similarities in shape, nature, and venation could be established, which would then help to distinguish them.

Fossil leaves, identified as those of *Lyonothamnus*, have been collected in various localities in the western United States from Washington to Oregon, California, and Nevada. The ages of all these fossil leaves range from Miocene to Pliocene. All the specimens collected so far are comparable to leaves of the extant *L. floribundus* Gray ssp. *asplenifolius* (Greene) Raven. The leaves of subspecies *asplenifolius* are so distinctive that similarities with the fossil forms are easily recognized (figs. 2, 4). So far, to my knowledge, no one has reported the presence of fossil leaves which may be comparable to foliage of subspecies *floribundus* (fig. 1).

The first fossil specimens to be identified as *Lyonothamnus* were collected by Axelrod in 1939 from the Tehachapi area of California; he